EXHIBIT 6

MINI REVIEW

Mosquito phytophagy – sources exploited, ecological function, and evolutionary transition to haematophagy

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Abstract

For a very long time, mosquitoes have been known or suspected to consume plant liquids. Recently eclosed mosquitoes cannot survive long without consuming sugary plant liquids that provide fuel for flight and enable blood-feeding and mating. Populations of even highly synanthropic mosquitoes may not be able to persist without phytophagy, even when vertebrate blood is readily available. Phytophagy is a key element of mosquito ecology, and understanding it is critical to combat mosquito-borne diseases. In this review, we summarize the current knowledge about mosquito phytophagy and outline future research needs. Specifically, we review the many plant-derived food sources mosquitoes exploit, study the pollination function of mosquitoes, highlight the predation risks of plant-foraging mosquitoes, investigate the role of microbes in the sugar-foraging ecology of mosquitoes, and shed light on the evolution of haematophagy.

Introductory remarks

To complete a gonotrophic cycle, the females of many mosquito species obtain vertebrate blood, a behaviour known as haematophagy; however, for a very long time, mosquitoes have also been known or suspected to consume plant liquids (Swammerdam, 1758; Ficalbi, 1899). It is now recognized that sugary plant liquids provide essential food for adult male and female mosquitoes (Foster, 1995; Stone & Foster, 2013; Nyasembe & Torto, 2014) which are considered at least partly phytophagous (Stone et al., 2018). Our broad definition of phytophagy in this review includes ingestion of nectar (nectarivory), fruit juices (frugivory), plant sap, and plant exudates.

Recently eclosed mosquitoes cannot survive long without consuming sugary plant liquids (Foster, 1995). These sugary plant meals provide fuel for flight and enable blood-feeding and mating (Foster, 1995). Blood-fed but sugar-deprived mosquitoes lay fewer eggs (Foster, 1995), have lower energy stores for overwintering (Foster, 1995), and are less able to mate (Stone et al., 2009, 2011). Populations of even highly synanthropic mosquitoes may not be able to persist without phytophagy, even when vertebrate blood is readily available (Stone et al., 2009).

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Phytophagy is a key element of mosquito ecology, and understanding it is critical to combat mosquito-borne diseases (Ferguson et al., 2010). Nonetheless, many questions regarding interactions between mosquitoes and plants remain. In this review, we summarize the current knowledge about mosquito phytophagy and outline future research needs. The review covers a wide range of distinct but interrelated topics which we have organized into sections A–G, each ending with a summary of the most salient points.

Section A: Is the term 'sugar-feeding' appropriate?

Plant sugars provide adult mosquitoes with vitally important energy for flight and survival (Foster, 1995). However, conceptualizing mosquitoes simply as plant 'sugar-feeding' is overly reductive. Mosquitoes also require non-carbohydrate nutrients including amino acids, salts, and vitamins that occur in nectar or other plant-derived fluids (Baker & Baker, 1973; Nicolson & Thornburg, 2007; Rivera-Pérez et al., 2017). Mosquitoes acquire these types of nutrients as part of their larval diet or from blood-feeding but also from plant-derived products (Rivera-Pérez et al., 2017). Amino acids added to synthetic nectar enhanced the survival of adult *Culex quinquefasciatus* Say females (Vrzal et al., 2010), and multivitamins added to a 10% sucrose or 10% glucose solution increased survivorship for

adult anopheline males in some species (Phasomkusolsil et al., 2017). Adult *Aedes aegypti* (L.) and *Culex pipiens* L. survived longer when they ingested the protein-rich nectar of *Impatiens walleriana* Hook. f. instead of a 10% sucrose solution or other plant nectar with lower protein content (but unknown sugar content) (Chen & Kearney, 2015). Polyphenols added to the diet of *A. aegypti* enhanced the autophagy in midgut cells, decreased midgut microbiota and increased mosquito longevity (Nunes et al., 2016). Moreover, adult female *A. aegypti* lived longer when they consumed aqueous extracts of pollen which can be present in nectar (Todd & Vansell, 1942) instead of a 10% sucrose solution, and some females even laid eggs when fed an aqueous extract of maize pollen, but not when fed a 10% sucrose solution (Eischen & Foster, 1983).

Plant fluids provide mosquitoes not only with energy but also with nutrition, to an extent that they can develop fertile eggs (Corbet, 1964; Eischen & Foster, 1983). Therefore, the term 'phytophagy', or 'host-plant feeding', rather than 'sugar-feeding', should be used to describe this acquisition of both carbohydrate and non-carbohydrate nutrients. The relative contribution of non-carbohydrate plant nutrients to nutrient provisioning of mosquito populations is not yet known.

Section B: Plant-derived food sources sought and consumed by mosquitoes

Floral nectar

Floral visitation by mosquitoes dates at least to the Cretaceous (Hartkopf-Froder et al., 2012) and many extant species visit a diverse array of inflorescences (see Peach & Gries, 2019). Floral nectar is the most important and most heavily utilized component of the phytophagous diet of adult mosquitoes (Foster, 1995, 2008; Stone & Foster, 2013; Nyasembe & Torto, 2014). Volatile floral and nectar semiochemicals (message-bearing chemicals) guide mosquitoes to nectar sources and help them discern inflorescences with varying nectar content (Manda et al., 2007; Foster, 2008; Schlein & Müller, 2008; Gouagna et al., 2010; Nyasembe et al., 2012; Gouagna et al., 2014; Nikbakhtzadeh et al., 2014, 2016; Nyasembe & Torto, 2014; Chen & Kearney, 2015; Yu et al., 2017, 2018). However, only few floral semiochemicals that guide mosquitoes have been identified (see Peach & Gries, 2019). They include alcohols, aldehydes, fatty acids, fatty acid derivatives, ketones, phenols, and terpenes (Nyasembe & Torto, 2014). The components that mosquitoes exploit to discern inflorescences and their nectar content are not known.

Semiochemicals are shared between plants and vertebrates (Nikbakhtzadeh et al., 2014; Lutz et al., 2017; Lahondère et al., 2019; Peach et al., 2019b) but the underlying mechanisms of resource discrimination by mosquitoes are not known. Findings that the same set of semiochemicals guides mosquitoes to different resources (Nikbakhtzadeh et al., 2014; Lahondère et al., 2019; Peach et al., 2019b) is evolutionarily significant. The concept that pollinators forage primarily for resources, not flowers specifically, has found support (Hoffmeister & Junker, 2017) and may also be applicable to mosquitoes. Shared resource cues imply that mosquitoes forage for resources in general, whether vertebrates or plants, and that vertebrate hosts (e.g., humans) are simply more attractive resources than others. Irrespectively, semiochemicals shared between resources cannot be resource indicators. Investigating cues that attract non-anthropophilic mosquitoes to inflorescences and to amphibian or avian hosts, or even to annelids (Reeves et al., 2018), may reveal the specific semiochemicals that serve as resource indicators.

Visual cues such as colour and contrast play a role for vertebrate-foraging mosquitoes, with dark colours usually being most attractive (Brown, 1951, 1954; Sippell & Brown, 1953; Wen et al., 1997; Chambers et al., 2013; Breugel et al., 2015). Visual floral cues are also thought to help attract nectar-foraging mosquitoes (Clements, 1999). Light-coloured flowers were most often frequented by mosquitoes (Sandholm & Price, 1962; Magnarelli, 1977, 1979), but the visual characteristics of those flowers were not measured. In contrast, oxeye daisies, *Leucanthemum vulgare* Lam., placed behind glass to eliminate odor cues, failed to attract mosquitoes, whereas inflorescences in the presence of floral scent, with and without visual cues, strongly attracted mosquitoes (Jepson & Healy, 1988). In the context of host-foraging, visual cues become attractive to mosquitoes when gated by olfactory cues (McMeniman et al., 2014; van Breugel et al., 2015; Vinauger et al., 2019). This concept may also apply to nectar-foraging mosquitoes. In the presence of floral scent, non-occluded inflorescences of common tansy, *Tanacetum vulgare* L., were more attractive to *A. aegypti* than occluded inflorescences (Peach et al., 2019b). The odor or CO_2 of a human observer may also have affected the responses of mosquitoes when they learned to associate light and dark shapes with sugar resources (Bernáth et al., 2016) and when they preferred dark artificial flowers over light-coloured alternatives (Dieng et al., 2018).

The many visual cues that attract pollinators and other floral visitors include inflorescence shape, colour, and colour patterns (Orbán & Plowright, 2014; Brodie et al., 2015). The circular 'bullseye' pattern on many flowers attracts pollinators and serves as a nectar guide, orientating insects to the centre of a flower once they have arrived (Free, 1970; Dinkel & Lunau, 2001). Bullseye patterns are often present in the UV range (Horovitz & Cohen, 1972),

and have been implicated in pollinator attraction in several systems (Horth et al., 2014; Koski & Ashman, 2014; Orbán & Plowright, 2014). Many insects including mosquitoes sense UV light (Muir et al., 1992; Briscoe & Chittka, 2001; Shimoda & Honda, 2013) and can read the pattern of UV-absorptive and -reflective petals. UV-absorptive (UV-dark) petals are attractive to mosquitoes (Peach et al., 2019c) which may explain the apparent contradiction that host-seeking mosquitoes are attracted to dark colours, whereas nectar-foraging mosquitoes reportedly visit human-visual white/yellow inflorescences.

Host body heat is a well-known attractant to host-foraging mosquitoes (Bowen, 1991; Olanga et al., 2010; McMeniman et al., 2014; van Breugel et al., 2015; Zermoglio et al., 2017), suggesting that floral heat too may affect nectar-foraging mosquitoes. A variety of mechanisms, including thermogenesis (Seymour & Schultze-Motel, 1997), focusing solar radiation (Hocking & Sharplin, 1965), and heat production by microbial metabolism of floral nectar (Herrera & Pozo, 2010) all enable inflorescences to become and stay warmer than their environment. Elevated inflorescence temperatures increase respiration and CO_2 production (Seymour et al., 2003, 2015; Seymour & Matthews, 2006), enhance semiochemical dissemination (Meeuse & Raskin, 1988), and generate a direct energy reward for pollinators (Seymour et al., 2003). Mosquitoes have been observed basking in the warm centres of heliotropic paraboloid-shaped flowers in the Canadian high arctic (Hocking & Sharplin, 1965), lending support to the concept that they do respond to thermal inflorescence cues.

CO_2 is another potential cue for plant-foraging mosquitoes. When diurnal photosynthesis ceases at dusk, plants become net CO_2 producers (Chapman et al., 1954; Allen, 1971; Amthor, 2000). Although this transition occurs during the peak plant-foraging time of many mosquito species (Andersson & Jaenson, 1987; Clements, 1999), their activity is still thought to be endogenously regulated (Clements, 1999). Vegetative CO_2 emission also results from increased respiration during thermogenesis (Seymour et al., 2003; Seymour & Matthews, 2006). Whether the rhythmic CO_2 pulses from some orchids (Hew et al., 1978) enhance attraction of mosquitoes is not known.

Extrafloral/extrasoral nectaries

Extrafloral/extrasoral nectaries (EFNs) also provide sugar for mosquitoes but their visitation is harder to track than floral visitation. Nonetheless, there are many reports of mosquitoes feeding from EFNs (see Peach & Gries, 2019). EFNs provide a survival benefit to mosquitoes (Gary & Foster, 2004), but little is known about the cues that attract mosquitoes to EFNs.

Extrafloral/extrasoral nectaries semiochemicals guide parasitoid wasps (Röse et al., 2006; Géneau et al., 2013). Of six headspace volatiles (benzaldehyde, benzyl alcohol, linalool, 1-octanol, two unknowns) originating from EFN nectar of fava bean, *Vicia faba* L., most were also found in leaves, but one of the two unknowns was specific to EFN nectar (Hoffmeister & Junker, 2017). Benzaldehyde, benzyl alcohol, and linalool are floral odorants attractive to mosquitoes (Jhumur et al., 2007; Yu et al., 2015), whereas 1-octanol causes flight aversion (von Oppen et al., 2015). Visual cues associated with EFNs are speculated to add to the attractiveness of EFNs (Hoffmeister & Junker, 2017).

Fruit and seedpods

Fruit-feeding behaviour of mosquitoes has been known or suspected for a long time (Swammerdam, 1758). However, unlike many herbivores, mosquitoes typically prefer damaged fruit to intact fruit. In the late 19th and early 20th centuries, many mosquito researchers fed their laboratory mosquito colonies on various fruit such as apple, banana, pear, plum, date, and wet raison (Smith, 1904; Howard et al., 1912; Bates, 1949; Chapman, 1962). Other authors reported field observation of mosquitoes feeding on fruit, including apple (Theobald, 1901; Joseph, 1970), grape, peach, and watermelon (Joseph, 1970), and possibly poke berry (Joseph & Bickley, 1969, in Joseph, 1970). Traps baited with cantaloupe, *Cucumis melo* L. var. *cantalupensis*, did capture mosquitoes but much fewer than in CO_2-baited traps (Reisen et al., 1986). In semi-field conditions, mango and guava nectar were generally not very effective attractants for *A. aegypti* but did attract small numbers of male mosquitoes (Fikrig et al., 2017).

The predilection for wild mosquitoes to feed on damaged, decaying, or fermenting fruit (Theobald, 1901; Joseph, 1970) has been validated by several studies, although feeding on intact (undamaged) seed pods has also been reported (Müller et al., 2010b). In Israel, *Aedes albopictus* (Skuse), *C. pipiens*, and *Culex perexiguus* Theobald were observed feeding on fermenting liquid from seed pods of the carob tree, *Ceratonia siliqua* L., previously damaged by moth larvae (Müller et al., 2010b). Some *A. albopictus* and *Culex* sp. individuals pierced intact carob seed pods to feed, whereas other *A. albopictus* fed on over-ripe, damaged sabra, *Opuntia ficus-indica* (L.) Mill. Field experiments revealed mosquito attraction to damaged *C. siliqua* seed pods with fermenting liquid but not to intact pods, as well as to damaged pomegranate, *Punica granatum* L., and to intact *O. ficus-indica*, *Ficus carica* L., *Eriobotrya japonica* (Thunb.) Lindl., and *Rubus sanctus* Schreb. (Müller et al., 2011). *Culex pipiens* subsp. *pallens* did feed on seed pods of white pear, *Pyrus bretschneideri* Rehd., and paper mulberry, *Broussonetia papyrifera* (L.)

Vent., but lived longer when feeding on select experimental flowers, and when feeding on *P. bretschneideri* seedpods instead of on a sucrose solution (Yu et al., 2016).

Fruit odours can be attractive to mosquitoes. Traps baited with cantaloupe, *C. m. cantalupensis*, did capture mosquitoes but much fewer than CO_2-baited traps (Reisen et al., 1986). In semi-field settings, mango and guava nectar were generally not very effective attractants for *A. aegypti* but did attract small numbers of male mosquitoes (Fikrig et al., 2017). Field experiments revealed mosquito attraction to damaged *C. siliqua* seed pods with fermenting liquid but not to intact pods, as well as to damaged *P. granatum* and to intact *O. ficus-indica*, *F. carica*, *E. japonica*, and *R. sanctus* (Müller et al., 2011).

Mosquitoes discern between decaying fruit and seedpods (Yu et al., 2017). Females of *C. p. pallens* showed the greatest preference for decaying seed pods of *Broussonetia papyfera* (L.) Vent., whereas males showed comparable preference for *B. papyfera* and decaying fruit of peach, *Amygdalus persica* L., and melon, *C. melo* (Yu et al., 2017). Artificial apple and cherry scents were attractive to *A. aegypti* (DA Carlson, unpubl., in Foster & Hancock, 1994) and synthetic strawberry flavouring was used as a mosquito attractant (Yee & Foster, 1992). Oranges and watermelons were as attractive to *Anopheles arabiensis* as a 10% sucrose solution (Tenywa et al., 2017).

Fresh or rotting/overripe mango, guava, honey melon, plums, nectarines, prickly pear cactus, as well as red wine and millet beer, have all been used in attractive toxic sugar baits (ATSBs) (Fikrig et al., 2017; Fiorenzano et al., 2017; Scott-Fiorenzano et al., 2017) which are designed to attract and kill mosquitoes. Whether the semiochemicals that guide mosquitoes originate from these resources themselves or from resource-dwelling microbes that aid in decomposition are not known but would make for an intriguing study. Moreover, the semiochemicals mediating the attraction of mosquitoes to fruit remain largely unknown, as do the semiochemicals causing differential attraction of specific mosquito species (Fikrig et al., 2017).

Plant tissues

Mosquitoes have been observed to occasionally feed directly on exudates of damaged plants (de Meillon et al., 1967; McCrae et al., 1969; Foster, 1995; Stone & Foster, 2013) and on tissue of intact plants (Schlein & Muller, 1995; Müller & Schlein, 2005; Qualls et al., 2013), obtaining sugar and other nutrients from tissue fluids or the phloem sap (Stone & Foster, 2013). Little is known about tissue fluid or phloem sap feeding and it may occur only when other resources are not available (Müller & Schlein, 2005), or when plants are injured or stressed (Stone &

Foster, 2013). Although plant tissue is not an ideal diet, it is widely available and can provide sufficient nutrition for a female mosquito to survive sufficiently long to complete at least one gonotrophic cycle (Qualls et al., 2013). The underlying mechanisms that attract mosquitoes to plant tissue are barely understood but recent electrophysiological recordings revealed several classes of plant chemicals that may be involved as well as species-specific sensitivity of mosquitoes to these chemicals (Nyasembe et al., 2018). Differential odour profiles of damaged and intact plants (Smith & Beck, 2013; Beck et al., 2015; Copolovici & Niinemets, 2016), and of water-stressed and well-watered plants (Copolovici & Niinemets, 2016; Salerno et al., 2017), may help mosquitoes select and feed on damaged or stressed plants (Junnila et al., 2010; Stone & Foster, 2013), which may offer more nutritional benefits to mosquitoes than healthy plants (Nunes et al., 2016). Applying molecular techniques, such as DNA barcoding, to identify plant genes in mosquito samples, holds great promise to determine the type of plant tissue mosquitoes feed on as well as the relative frequency of their plant feeding (Nyasembe et al., 2018).

Honeydew

Honeydew is a sugary plant-derived liquid excreted by aphids, coccids, and other hemipterans feeding on plant sap. It is a food-source exploited by many insects including ants, honeybees (Auclair, 1963), and mosquitoes (Haegar, 1955; Burkett et al., 1999; Russell & Hunter, 2002; Gary & Foster, 2004). Both honeydew and floral nectar contain various sugars and amino acids (Auclair, 1963; Hussain, Forrest & Dixon, 1974; Blüthgen et al., 2004; Pozo et al., 2014). The composition of honeydew varies with the species and the age of the insect producing it, and the host plant it is feeding on (Fischer et al., 2002; Blüthgen et al., 2004; Pringle et al., 2014).

Captures of mosquitoes in a sand pine, *Pinus clausa* (Chapm. ex Engelm.) Sarg., infested with aphids, but not in another nearby pine void of aphids, were attributed to honeydew on the infested pine (Clouse et al., 1997). In Florida (USA), *Aedes taeniorhynchus* (Wiedemann), *Aedes sollicitans* (Walker), and *Anopheles atropos* Dyar & Knab were all observed feeding on honeydew from unspecified aphids residing on the leaves of Spanish needle, *Bidens* spp. (Haegar, 1955). In North Central Florida, almost 60% of wild-caught *Anopheles quadrimaculatus* Say and 31% of *Culiseta melanura* (Coquillett) tested positive for honeydew feeding (Burkett et al., 1999), whereas in Canada, aedine mosquitoes had little evidence for honeydew feeding (Russell & Hunter, 2002). Intriguingly, neurones on the labella of *Anopheles gambiae* Giles can sense melezitose (Kessler et al., 2015), a main sugar component of some

honeydews (Fischer & Shingleton, 2001; Blüthgen et al., 2004).

Honeydew odorants guide many insects to honeydew itself or the insect expelling it (e.g., Hung et al., 2015). Odorants in honeydew expelled by scale insects on New Zealand's South Island attract the common yellow jacket, *Vespula vulgaris* (L.), which is invasive in New Zealand (Brown et al., 2015). Microbes dwelling in aphid honeydew produce semiochemicals that attract the predatory hoverfly *Episyrphus balteatus* (De Geer) (Leroy et al., 2011). Field observations that neither *C. pipiens* nor *A. albopictus* responded to honeydew-soiled plants (Schlein & Müller, 2008; Müller et al., 2011) were attributed to exogenous microbes and their semiochemicals still absent from that honeydew. A role of microbe-derived honeydew semiochemicals was evident in a recent study (Peach et al., 2019a) showing that synthetic semiochemical blends of microbe-infested honeydew were more attractive than those of sterile honeydew. The same study also demonstrated anemotactic attraction of *A. aegypti* to bean plants, *V. faba*, soiled with honeydew from pea aphids, *Acyrthosiphon pisum* (Harris), and green peach aphids, *Myzus persicae* (Sulzer). Several types of honeydew may have more nutritional value than certain types of floral nectar to at least some mosquito species. *Anopheles gambiae* survived better on mealybug honeydew than on floral and extra-floral nectar of several plants (Gary & Foster, 2004), and *C. quinquefasciatus* survived longer on aphid-infested plants than on aphid-free plants (Patterson et al., 1969). In the diet of some mosquitoes, honeydew may play a particularly important role because it may be available at times when widely used sources of plant-derived food, such as floral nectar, are absent. The nutritional benefit honeydew provides its attractiveness relative to other plant-derived food sources, and the circumstances that prompt its consumption are all yet to be studied.

Ant regurgitate

As a form of remarkable kleptoparasitism, regurgitate of *Cremastogaster* spp. ants that feed on honeydew or extrafloral nectar becomes a food source for *Malaya* spp. mosquitoes (Clements, 1999). When a female mosquito inserts her proboscis into the mouth of an ant, she induces trophallaxis and then feeds upon the ant's regurgitate (Edwards, 1932). Repeated encounters and mutual disturbance of *Hodgesia* mosquitoes and ants at damaged-plant-tissue feeding sites (McCrae et al., 1969), or mosquito consumption of honeydew in the presence of ants (Clouse et al., 1997), may indicate events or circumstances that have given rise to the evolution of this form of kleptoparasitism. Whether also

mosquito males kleptoparasitize the ants, and the cues mosquito females exploit to locate these ants, has yet to be investigated.

Sweet food waste

Consumption of sweet food waste, such as sugary cakes, by laboratory-reared mosquitoes (Dieng et al., 2017) increased their longevity (Dieng et al., 2017). The phenomenon is analogous to wild mosquitoes feeding on honeydew or on damaged plant tissue (de Meillon et al., 1967), and indicates that proper sanitation and disposal of food waste is one tactic to help curtail mosquito populations.

Summary

Mosquitoes commonly exploit plant semiochemicals to locate plant-based food sources. Foraging mosquitoes also respond to visual plant cues (e.g., floral UV pattern), vegetative CO_2, and thermal inflorescence cues. Plant-based food sources most attractive to mosquitoes offer often, but not always, rich rewards of sugar or non-energy nutrients (Chen & Kearney, 2015; Nikbakhtzadeh et al., 2016; Yu et al., 2016). Neither the airborne semiochemicals that guide mosquitoes to plant resources nor the non-volatile phagostimulants that induce probing and feeding have been intensely studied. Plant semiochemicals that effectively guide mosquitoes in the laboratory may not be equally effective in more complex field settings.

Section C: Do mosquitoes have a functional role as pollinators?

Floral visitation by mosquitoes is wide-spread and well-documented (Foster, 1995; see Peach & Gries, 2019). However, the functional role of mosquitoes visiting inflorescences has hardly been studied. Context-specific, mosquitoes are considered nectar thieves (consuming nectar without transferring pollen), nectar robbers (piercing through inflorescences to access nectar; Inouye, 1980), or legitimate pollinators. As nectar thieves and nectar robbers, mosquitoes have adverse impact on the reproductive fitness of plants (Irwin et al., 2010; Zhang et al., 2014).

Instances of nectar theft

Claims that mosquitoes are nectar thieves are supported only by few observations (Smith & Gadawski, 1994; Otienoboru et al., 2012; Pansarin & Pansarin, 2017). *Aedes provocans* (Walker) feeding on nectar of pin cherry, *Prunis pensylvanica* L. f., were deemed nectar thieves because they hardly accumulated pollen on their body and failed to contact floral pistals (Smith & Gadawski, 1994). Mosquitoes feeding on common milkweed, *Asclepias syriaca* L., and on

the orchid *Epidendrum avicula* Lindl. were also considered nectar thieves due to their small body size (Otienoburu et al., 2012; Pansarin & Pansarin, 2017). Mosquitoes were observed nectar robbing the stinking-bean trefoil, *Anagyris foetida* L. (Ortega-Olivencia et al., 2005), and possibly the creeping thistle, *Cirsium arvense* (L.) Scop. (Britten, 1937).

Evidence for pollination

Pollination by mosquitoes is unequivocal. According to various studies, *C. pipiens* transfer pollen between inflorescences of the mosquito flower, *Lopezia racemosa* Cav. (Müller, 1873); *C. pipiens* and *Culiseta annulata* (Schrank) pollinate the Spanish catchfly, *Silene otites* (L.) Wibel ex Sm. (Brantjes & Leemans, 1976); *C. pipiens* pollinate the common tansy, *T. vulgare* (Peach & Gries, 2016), yarrow, *Achillea millefolium* L. (DAH Peach, unpubl.), and carry pollen of Canada goldenrod, *Solidago canadensis* L., which may also be pollinated by *Culex tarsalis* Coquillett and *Culiseta incidens* (Thomson) (Peach & Gries, 2016).

The small northern bog orchid, *Platanthera obtusata* (Banks ex Pursh) Lindl., is pollinated by *Aedes* spp. (Raup, 1930; Twinn et al., 1948; Hocking et al., 1950; Stoutamire, 1968; Thien, 1969; Thien & Utech, 1970; Gorham, 1976; Lahondère et al., 2019), taxonomically unspecified mosquitoes (Dexter, 1913), and by *Aedes campestris* Dyar & Knab in the Yukon Territory (DAH Peach, pers. obs.). *Aedes* spp. also pollinate other orchids including the pale-green orchid, *Platanthera flava* (L.) Lindl. (Stoutamire, 1971; Luer, 1975), the northern green orchid, *Platanthera hyperborea* Lindl. (D Saville, pers. comm. in Catling & Catling, 1991), and possibly the slender bog orchid, *Platanthera stricta* Lindl. (Patt et al., 1989). Moreover, *Aedes* spp. along with *Anopheles anulipes* Walker and possibly *Culex* spp. pollinate the green labellum orchid, *Pterostylus procera* Jones & Clem. (Bartareau & Jackes, 1994), and *Culex* spp. pollinate the nodding greenhood orchid, *Pterostylus falcata* Rogers (Coleman, 1934; Hyett, 1960), as well as the pointed greenhood orchid, *Pterostylus acuminata* R Br (Coleman, 1934). Orchids in New Zealand are visited by small taxonomically unspecified Culicidae (Thomson, 1927). *Aedes* spp., probably *Aedes impiger* (Walker) and *Aedes nigripes* (Zetterstedt) (Hocking & Sharplin, 1965; Wood, Dang & Ellis, 1979), contribute to the pollination of the white mountain-avens, *Dryas integrifolia* Vahl, in the Canadian high arctic (Kevan, 1972). *Culex* spp. and *Armigeres* spp. were deemed exclusive pollinators of *Burmannia lutescens* Becc., *Gnetum cuspidatum* Blume, and *Sciaphila secundiflora* Thwaites ex Benth. because of a morphological congruence between their proboscis and the corolla tube length of these plants (Kato, 1996).

Conceptually, the pollination function of mosquitoes may take one of the three forms. Mosquitoes may be (1) somewhat specialized pollinators or co-pollinators together with small moths, (2) co-pollinators together with other dipterans (myophily), and (3) generalist pollinators. Mosquitoes are exclusive pollinators of *B. lutescens* (Kato, 1996). Together with moths, they co-pollinate the orchids *P. obtusata* and *P. flava* (Stoutamire, 1968; Voss & Riefner, 1983) and the catchfly *S. otites* (Brantjes & Leemans, 1976). Together with flies they co-pollinate the mosquito flower, *L. racemosa* (Müller, 1873; Eyde & Morgan, 1973), the short-lipped greenhood, *P. procera* (Bartareau & Jackes, 1994), and *S. secundiflora* (Kato, 1996). As generalist pollinators, mosquitoes together with many other insects contribute to the pollination of tansy, *T. vulgare* (Peach & Gries, 2016), yarrow, *A. millefolium* (DAH Peach, unpubl.), and *D. integrifolia* (Kevan, 1972).

Interestingly, some mosquito-pollinated orchids are visually inconspicuous and scentless to humans. Both mosquitoes and lepidopterans can sense CO_2 which some orchids emit in rhythmic pulses (Hew et al., 1978). CO_2 pulses might serve as foraging cues to mosquitoes visiting *P. obtusata* (Stoutamire, 1968). Experimentally tested, CO_2 also enhanced the attraction of *A. aegypti* to tansy odorants (Peach et al., 2019b). Growing gregariously may be advantageous for plants as their mosquito or lepidopteran pollinators can access them by short flights or walks (Brantjes & Leemans, 1976).

Summary

Mosquitoes are nectar thieves but also pollinators for many plants. Compared to other insects, mosquitoes may be less effective at carrying and transferring pollen, but by virtue of large numbers they may assume an important pollination role (Larson et al., 2001).

Section D: Predation risk of plant-foraging mosquitoes

Blood-feeding mosquitoes are often killed by their vertebrate hosts (Corbet & Downe, 1966; Edman & Kale, 1971; Edman et al., 1984) but nectar-feeding mosquitoes are also subject to increased predation risk. Predators such as goldenrod crab spiders, *Misumena vatia* (Clerck), ambush mosquitoes visiting flowers (Peach & Gries, 2016). Predators have both a direct and an indirect impact on pollinators in that they reduce their numbers and modulate the energy they invest in predator avoidance (Reader et al., 2006), thereby possibly reducing their fitness (Reader et al., 2006).

Section E: The role of microbes in attracting mosquitoes to plant resources

Insect-microbe inter-kingdom signalling is widespread (Davis et al., 2013) and also involves mosquitoes. Mosquitoes respond to microbial semiochemicals or CO_2 when they seek vertebrate hosts (Verhulst et al., 2009, 2010; Busula et al., 2017; Takken & Verhulst, 2017), floral nectar (DAH Peach, unpubl.), aphid honeydew (Peach et al., 2019a), and oviposition sites (Ponnusamy et al., 2008).

Microbes commonly inhabit inflorescences (Endo et al., 2011; Aleklett et al., 2014; Ushio et al., 2015) and their nectar (Álvarez-Pérez et al., 2012; Fridman et al., 2012), and produce semiochemicals that help attract insect pollinators (Pozo et al., 2014; Rering et al., 2018). For instance, the presence of the nectar specialist and nectarivorous yeast *Metschnikowia reukaufi* Pitt & MW Mill. increases the number of bumblebee visits to inflorescences of the stinking hellebore, *Helleborus foetidus* L. (Herrera et al., 2013). Odorants of *M. reukaufi* alter the floral scent composition of the sticky catchfly, *Silene caroliniana* Walter (Golonka et al., 2014). 3-Methyl-1-butanol as one of these microbial attractants is also produced by the human skin microbe *Staphylococcus epidermis* (Winslow & Winslow) Evans (Verhulst et al., 2009, 2010). Inflorescence-dwelling microbes also generate heat (Herrera & Pozo, 2010) and CO_2 (Smallegange et al., 2010) which are both attractive to mosquitoes.

Microbe-mediation is likely also responsible for the attraction of mosquitoes to rotting and fermenting fruit (Theobald, 1901; Joseph, 1970; Müller et al., 2010a, 2011; Yu et al., 2017), and to fruit previously been fed upon by hymenopterans (Joseph, 1970) that vector semiochemical-emitting microbes between food sources (Davis et al., 2012).

Metabolites and semiochemicals of microbes dwelling in or on nectar, pollen, honeydew, fruit, or other types of host-plant food could inform mosquitoes about the nutritional quality of a resource. Mosquitoes can acquire microbes from floral nectar or floral nectar surrogates (Maier et al., 1987; Kenney et al., 2017) and transmit them between nectar sources (Kenney et al., 2017), as many other insects do (Ushio et al., 2015).

Summary

Microbe-derived semiochemicals guide mosquitoes to vertebrate hosts, floral nectar, aphid honeydew, and suitable oviposition sites. Few studies have addressed 'signalling' between plant-dwelling microbes and mosquitoes.

Section F: The evolution of haematophagy in mosquitoes

Haematophagy by insects is thought to have arisen multiple independent times (Lehane, 2005) and to have evolved from either entomophagy or phytophagy involving an association between either ancient insect prey and vertebrates, or plant matter and vertebrates (Lehane, 2005). This association is further thought to have eventually led to accidental feeding on vertebrates, subsequent physiological adaptation by mosquitoes to process blood meals, and finally to the evolution of associations between the now haematophagous mosquitoes and their vertebrate hosts (Lehane, 2005).

According to the rare field observations of mosquitoes engaging in entomophagy, mosquitoes fed on a cicada, the chrysalis of a butterfly, and on small dipterans (Howard et al., 1912). However, Downes (1958) considers the former two instances accidental and the latter a misinterpretation of Hagen (1883). According to another field report (Eliason, 1963), *C. tarsalis* females fed on the dry remains of an insect that had impacted on a car window. Entomophagy by female mosquitoes has more often been observed in the laboratory. Females of *A. aegypti* and *C. tarsalis* feeding on various soft-bodied lepidopteran larvae experienced mixed effects on their survival and egg development (Harris & Cooke, 1969; Harris et al., 1969). In Y-tube-olfactometer bioassays, female but not male *Anopheles stephensi* Liston were attracted to insect larvae, likely in response to larval respiratory CO_2 (Martel et al., 2011; George et al., 2014).

Anthophilous nematocerans such as early mosquitoes were possible pollinators of primitive angiosperms (Labandeira, 1997; Larson et al., 2001). Fossil evidence of floral visitation by mosquitoes in the mid-Cretaceous (Hartkopf-Froder et al., 2012), and genetic evidence for rapid radiation in mosquito diversity corresponding with the appearance and radiation of angiosperms (Reidenbach et al., 2009), all suggest an ancient relationship between mosquitoes and plants. Phytophagy (e.g., consumption of host-plant nectar, fruit, tissue) is considered one possible diet from which haematophagy evolved in mosquitoes (Mattingly, 1965; Foster, 1995; Pawlowski et al., 1996; Lehane, 2005), and possibly other haematophagous nematoceran dipteran families (Mattingly, 1965). The elongate mouthparts of mosquitoes may have first arisen as a means of reaching the base of tubular corollas to obtain nectar (Foster, 1995; Larson et al., 2001). Primarily frugivorous noctuid moths (*Calyptera* spp.) appear to be in the process of evolving haematophagy (Bänziger, 1975, 1979; Zaspel et al., 2007, 2012; Hill et al., 2010). This evolutionary process may be linked to differences in sensillum numbers

between haematophagous and non-haematophagous individuals and chemoselectivity towards vertebrate-related odorants (Hill et al., 2010).

Plant-feeding mosquito ancestors that possessed elongate sucking mouthparts would have been pre-adapted to haematophagy, requiring only an impetus to be in continual association with vertebrate hosts and to accidentally bite them (Lehane, 2005). Attractive odorants shared between floral and vertebrate headspaces, as well as CO_2 being a resource indictor of both vertebrate hosts (Gillies, 1980) and floral nectar (Peach et al., 2019b), all provide evidence of intriguing overlap in those cues that mosquitoes exploit to locate food plants and vertebrate hosts. This overlap in foraging cues may have been a contributory cause for the shift from phytophagy to haematophagy and may also support the argument that phytophagy pre-empted haematophagy in ancient mosquitoes or their ancestors (Peach et al., 2019b).

The ability of female mosquitoes feeding on laboratory-reared lepidopteran larvae to develop and lay eggs (Harris & Cooke, 1969) has received much attention. However, these females were provisioned with a sugar source in form of honey water and honey water controls were not run. Furthermore, many mosquito species in the laboratory or field require a meal of plant fluids to maximize egg production or even to develop eggs (O'Meara, 1987). Moreover, when *A. aegypti* females were provisioned with pollen, or an aqueous extract thereof, they were able to develop and lay eggs without consuming vertebrate blood (Eischen & Foster, 1983).

The ancient mecopteran-like insects currently believed to be the ancestors of the Diptera possessed mandibular mouthparts and may have been entomophagous (Waage, 1979), comparable to the modern-day entomophagous insects that also feed on aphid honeydew or nectar from extra-floral nectaries (Way, 1963; Heil, 2015). Fossil records of early mosquitoes are sparse (Poinar et al., 2000; Borkent & Grimaldi, 2004, 2016; Briggs, 2013) and lack useful information, although it does seem that vertebrate blood-feeding mosquitoes existed at least 46 million years ago (Greenwalt et al., 2013). The appearance of lepidopterans in the fossil record prior to the currently accepted arrival date of angiosperms (van Eldijk et al., 2018) also raises the intriguing possibility that nectar-like substances may have been sufficiently common to allow for adaptive radiation based on plant-derived food-sources prior to the appearance of floral nectaries.

Changes in dietary regimes in mosquitoes may be the result not of single but multiple transitions, such as the ones from entomophagy to phytophagy and then to combined phytophagy and haematophagy. They may also include the loss of adult feeding, as seen in some sister taxa

of the Culicidae (Grimaldi & Engel, 2005), and subsequent re-acquisition of adult feeding, possibly in different dietary regimes. Ultimately, additional fossil specimens are needed to fully elucidate mosquito evolution.

Summary

Haematophagy in mosquitoes likely evolved from either entomophagy or phytophagy. Entomophagy by female mosquitoes has been observed in the laboratory but not in the field. Mosquito phytophagy is ancient. Overlap in vertebrate host and floral cues that foraging mosquitoes exploit to locate resources may be part of the underlying mechanisms that facilitated the adoption of haematophagy to the phytophagous diet.

Section G: Exploiting mosquito phytophagy for monitoring and control of mosquito populations

The phytophagous behaviour of mosquitoes can be exploited in the design of innovative and complementary tactics for monitoring and control of mosquito populations. In particular, dissemination of plant-based odorants, alone or in combination with host-based odorants, would facilitate attraction and capture of mosquitoes that – due to their age or physiological stage – are not receptive to vertebrate host cues (Foster, 2008). Capturing mosquitoes of any age or gonotrophic stage would help disrupt the transmission cycle of pathogens carried by female mosquitoes. Plant odorants also attract mosquito males offering an improved tool for monitoring the presence and abundance of particular mosquito species (Foster, 2008).

Attractive toxic sugar baits

Fresh, rotting, or overripe fruit such as mango, guava, honey melon, plum, nectarine, prickly pear cactus, as well as red wine and millet beer, have all been used in ATSBs which were designed to attract and kill mosquitoes seeking sugary plant fluid (Fikrig et al., 2017; Fiorenzano et al., 2017; Scott-Fiorenzano et al., 2017). ATSBs are devised by mixing fruit or nectar with sugar, a lethal agent, a preservative, and occasionally a source of microbes (Fiorenzano et al., 2017). ATSBs seem to have limited effect on non-target insects (Fiorenzano et al., 2017) but more studies in diverse ecological settings are required to draw definitive conclusions about the impact of ATSBs on mosquitoes and on non-targets.

Honey cards

For decades, sentinel animals have been deployed as mosquito baits to monitor for transmission of mosquito-borne pathogens. Deployment of non-animal baits, instead of sentinel animals, would accomplish the same objective in

more humane, less expensive, and more efficient ways. When a mosquito infected with a pathogen, such as the malaria parasite *Plasmodium falciparum* Welch or Dengue or Zika virus, is feeding on a host, it expels its saliva together with the pathogen into the host (Doggett et al., 2001; van den Hurk et al., 2007), a process termed expectoration. Techniques to detect the presence of pathogens in mosquito saliva expectorated into plant sugar or fluids at bait stations are being developed and show promise in both laboratory and field settings (Ramírez et al., 2018). Both West Nile Virus expectorated by mosquitoes into sucrose-soaked cotton wicks, and Dengue virus and *P. falciparum* expectorated into honey-covered nucleic acid preservation cards, were detectable in laboratory studies (Brugman et al., 2018; Danforth et al., 2018; Melanson et al., 2018). Moreover, field-deployed honey-baited nucleic acid preservation cards revealed the presence of expectorated arboviruses (Hall-Mendelin et al., 2010; Flies et al., 2015), thus demonstrating the potential for operational implementation of this technique for detection of mosquito-borne pathogens. Indeed, sugar bait stations may reveal the presence of mosquito-borne pathogens sooner than sentinel animals (Lothrop et al., 2012). However, this method has yet to be shown effective for field detection of *P. falciparum*.

Synthetic plant scent may enhance the attractiveness of honey baits (Lothrop et al., 2012; Steiner et al., 2018) but field studies comparing the efficacy of scented and unscented baits for arbovirus detection are still required. Furthermore, the odour profile of honey differs according to its botanical origin (Cuevas-Glory et al., 2007), and the type of honey most attractive to mosquitoes is still not known. Of potential concern is that the mosquitoes feeding on sugar pads harboring West Nile virus at a titre of 10^7 plaque-forming units per ml were then infected with this virus (Lothrop et al., 2012). This titre is greater than that generally present in the saliva of West Nile virus-positive *Culex* spp. (Colton et al., 2006) but the results nonetheless indicate an intriguing possible role of pathogen-infested natural sugar solutions in pathogen transmission dynamics.

Interactions between mosquitoes, plants, and pathogens

Plant species composition and abundance affect the availability of plant sugar or non-carbohydrate nutrients which, in turn, affect the number of mosquitoes that survive sufficiently long for pathogens to replicate and for mosquitoes to become infectious. The abundance and quality of host-plant resources are linked to the changes in mosquito survival and vectorial capacity (Stone et al., 2018). Selective removal of plants that – nutritionally – are particularly beneficial to mosquitoes may help curtail

mosquito populations (Stone et al., 2018) but this tactic should first be field-tested in various contexts (e.g., high vs. low availability of alternate food sources) before it becomes part of any mosquito integrated pest management strategy. Indiscriminate mass-removal of native host-plants has likely adverse effects on native non-target organisms, may change local micro-climates, cause erosion, and alter landscape aesthetics. However, altering the density and spatial distribution of just the highly nutritious host plants would still contribute to mosquito or pathogen management (Zhu et al., 2015) and allow ample vegetation to remain in place. This tactic could have the added benefit of prompting sugar-foraging mosquitoes to leave domiciles (Zappia et al., 2018) and of reducing the likelihood for the development of behavioural resistance to insecticide-treated bed nets (Stone et al., 2016).

Significant knowledge gaps in this field of research remain. Most if not all studies in this field have worked with *Anopheles* spp. and malaria parasites (Stone & Foster, 2013; Stone et al., 2018). Knowledge obtained from these studies may or may not be applicable to culicine mosquitoes or to mosquito species with vastly different life-history traits or pathogen infections. It also remains unknown whether and to what extent the removal of mosquitoes from plant and animal communities will impact plant pollination and food resources for insectivorous animals.

Plant-odour lures

Plant-odour lures offer many benefits over host-odour lures for mosquito attraction and capture, including the attraction of males and females irrespective of their age and gonotrophic stage (Foster, 2008). Plant-odour lures can be combined with other types of lures (Fikrig et al., 2017; Jacob et al., 2018) including CO_2 (Nyasembe et al., 2015; Peach et al., 2019b) but may be effective even without CO_2 (Foster, 2008).

Interestingly, some odour blends perform differently in laboratory and field settings (Jacob et al., 2018), indicating the importance of field testing. There is also a paucity of information on plant odorants that attract mosquitoes to plant food sources (Nyasembe & Torto, 2014; Torto, 2019) or help them discern plant food sources (Torto, 2019). Identifying these odorants may provide new opportunities for the development of potent mosquito lures.

Summary

The phytophagous behaviour of mosquitoes can be exploited in the design of innovative and complementary tactics for monitoring and control of mosquito populations. Plant-based lures, alone or in combination with vertebrate-based lures, would facilitate attraction and

capture, or toxic-bait exposure, of both male mosquitoes and female mosquitoes irrespective of their age and gonotrophic stage. Technologies to detect the presence of pathogens in mosquito saliva expectorated into sugar bait stations are being developed and show promise, but further field testing of both reliable pathogen detection and impact on non-target organisms are needed. These technologies may eventually replace sentinel animals that have been deployed for decades to monitor for transmission of mosquito-borne pathogens.

Conclusion

Many aspects of the phytophagous foraging ecology of mosquitoes remain unexplored or underexplored. Field studies ought to investigate the (1) interaction between mosquitoes and plants (e.g., pollination), (2) effect of phytophagy on the vectorial capacity of mosquitoes, (3) mechanisms by which mosquitoes discern sources of plant-derived nutrition, and (4) semiochemical and visual cues that attract mosquitoes to these resources. As mosquitoes are not monolithic, a better understanding of species-specific foraging tactics and dietary needs may tailor and optimize efforts for mosquito control. We should also acknowledge that mosquitoes are often viewed through an anthropocentric lens that is focused on their haematophagy and disease transmission. Adopting the paradigm that mosquitoes are first and foremost phytophagous may offer new avenues for research and ultimately control of mosquito populations.

Acknowledgements

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